The Veliger 36(4):389–398 (October 1, 1993)

THE VELIGER

Atlanta californiensis, a New Species of Atlantid Heteropod (Mollusca: Gastropoda) from the California Current*

by

ROGER R. SEAPY

Department of Biological Science, California State University–Fullerton, Fullerton, California 92634, USA

AND

GOTTHARD RICHTER

Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt a.M. 1, Germany

Abstract. A new species of atlantid heteropod, *Atlanta* ***californiensis,*** from California Current waters off southern California is described on the basis of external and internal shell structure and eye, opercular, and radular morphologies. Although the external shell structure of *A.* ***californiensis*** is most similar to that of *A. gaudichaudi,* all other morphological features examined ally it most closely with *A. inflata.* The geographical distribution of *A.* ***californiensis*** is within the Transition Zone faunal province of the North Pacific Ocean. Other authors have rejected use of the radula as a taxonomic character in the Atlantidae. This is undoubtedly due to misinterpretation of differences within the radula that result from radular ontogenesis. When only the adult portion of the radula is used, interspecific differences are evident.

INTRODUCTION

In an extensive survey of the heteropod molluscan fauna of the California Current between about 24° and 44.5°N latitude, McGowan (1967) reported five species of atlantids. In order of decreasing abundance, they included *Atlanta peroni* Lesueur, 1817, *A. lesueuri* Souleyet, 1852, *A. gaudichaudi* Souleyet, 1852, *A. inflata* Souleyet, 1852, *A. inclinata* Souleyet, 1852, and *A. turriculata* d'Orbigny, 1836. Specimens that could not be identified as one of the above species were referred to *Atlanta* sp. (J. McGowan, personal communication). Along with *A. peroni, Atlanta* sp. was the most abundant atlantid and ranged over nearly the entire CalCOFI station grid. The species of *Atlanta* described herein is the most abundant and often the only species of atlantid collected from the plankton off the coast of southern California (R. Seapy, unpublished data). Thus, it is probable that a large portion of McGowan's *Atlanta* sp. is this previously undescribed species. Unfortunately, the specimens of atlantids from McGowan's study no longer exist (J. McGowan, personal communication).

Types and voucher specimens of *Atlanta* ***californiensis*** sp. nov. have been deposited in the Santa Barbara Museum of Natural History, Santa Barbara, California (SBMNH); California Academy of Sciences, San Francisco, California (CASIZ); National Museum of Natural History, Washington, D.C. (USNM); and Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt, Germany (SMF). Additional specimens are in the collections of A. L. Alldredge (ALA) and the authors (R. R. Seapy, RRS, and G. Richter, GR).

Atlanta ***californiensis*** Seapy & Richter, sp. nov.

(Figures 1–11)

Material examined: 134 juveniles, mature males and females, 0.7–2.5 mm diameter; California, Santa Catalina

* Contribution 71, Ocean Studies Institute, California State University.

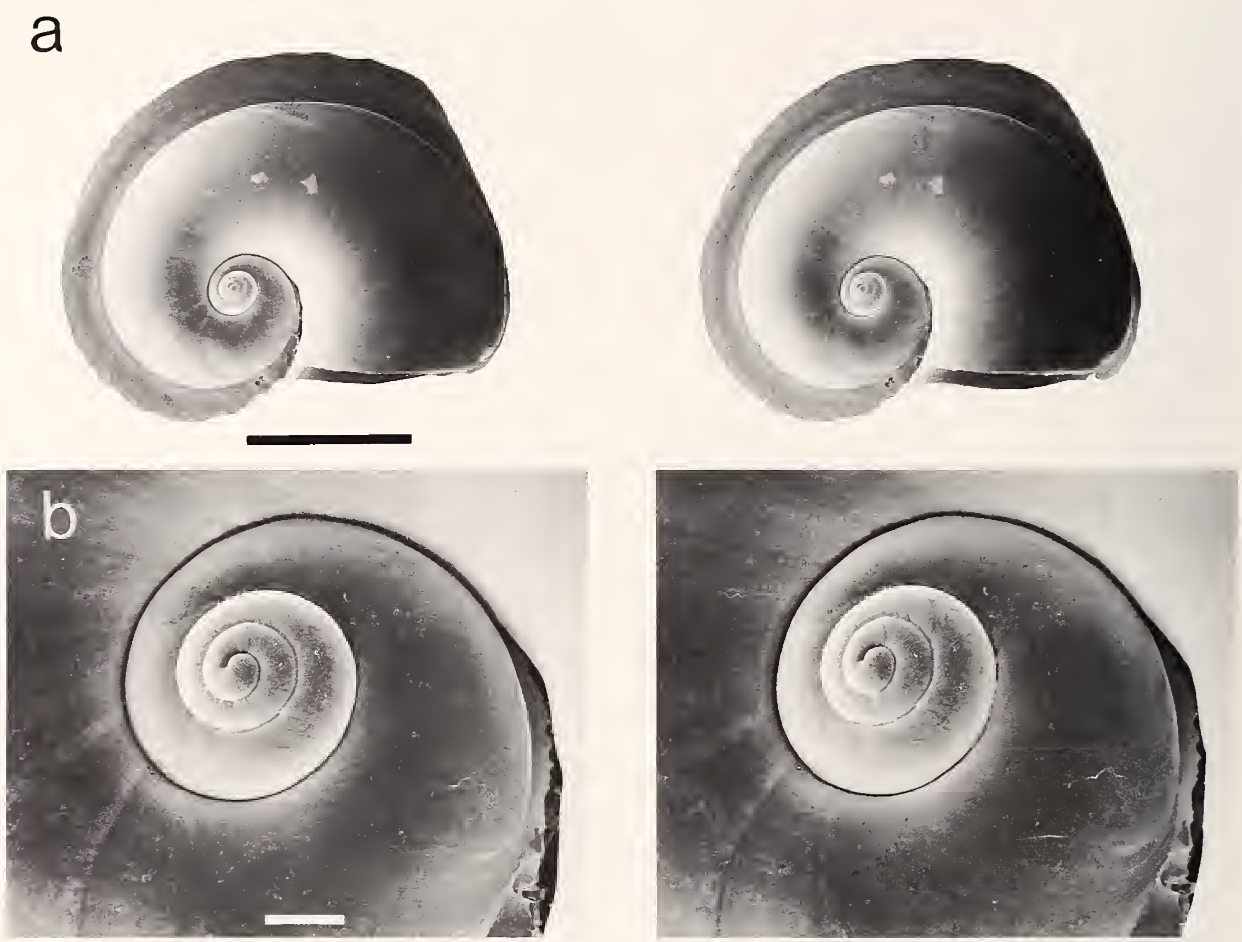


Figure 1

Atlanta ***californiensis*** sp. nov. Stereo-pair SEM photographs of holotype shell perpendicular to shell plane viewed from right side (2.48 mm, female; SBMNH 140126). Scale bars = a: 1.0 mm; b: 0.1 mm.

Basin, 33°03.4′N, 118°24.7′W, 0–150 m (oblique tow); *coll.* R. R. Seapy, California State University Ocean Studies Institute, R/V *Yellowfin,* 1-m plankton net (0.5-mm mesh), 29 August 1991, 1405–1435 hr; RRS (uncatalogued).

—766 juveniles, mature males and females, 0.6–2.7 mm diameter; CALIFORNIA, San Pedro Basin, 33°30.2′N, 118°25.5′W, 0–290 m (oblique tow); *coll.* R. R. Seapy, California State University Ocean Studies Institute, R/V *Yellowfin,* 3-m^2 plankton net (0.5-mm mesh), 13 August 1989, 1252–1400 hr; RRS (uncatalogued).

—126 juveniles, mature males and females, 0.6–3.2 mm diameter; CALIFORNIA, Santa Barbara Basin, 34°10′N, 119°45′W, 40 m (1800–1815 hr), 30 m (1830–1845 hr) and 15 m (2345–2400 hr); *coll.* A. L. Alldredge, University of California, Santa Barbara, R/V *Point Sur,* 70-cm BONGO nets (0.5-mm mesh), 4 October 1990; ALA (uncatalogued).

—8 mature males, 1.2–2.5 mm diameter; NORTH PACIFIC OCEAN, Subarctic Boundary, 43°15′N, 165°00′W, surface neuston tow; *coll.* National Marine Fisheries Service personnel, R/V *Melville,* Station 108, Manta net (0.5-mm mesh), 22 October 1989, 1834–1849 hr; RRS (uncatalogued).

—2 juveniles and 2 mature females, 0.6–2.5 mm diameter; NORTH PACIFIC OCEAN, off British Columbia, 49°35′N, 127°44′W, 0–250 m (oblique tows); *coll.* Institute of Ocean Sciences, Ocean Ecology, Sidney, British Columbia personnel, Station SK-7, Cruise 9003, Series 28 (2.5-mm female) and Cruise 9006, Series 21 (remaining specimens), 70-cm BONGO nets, 16 October 1990; RRS (uncatalogued).

Diagnosis: A species of *Atlanta* Lesueur with a flattened, transparent calcareous shell and keel. Spire of shell low and globular; surface smooth, with 4¼ whorls; whorl width increases rapidly in fourth whorl. Suture separating spire whorls shallow. Umbilicus deep and wide. Last whorl encircled by keel that is high and truncate along its anterior margin.

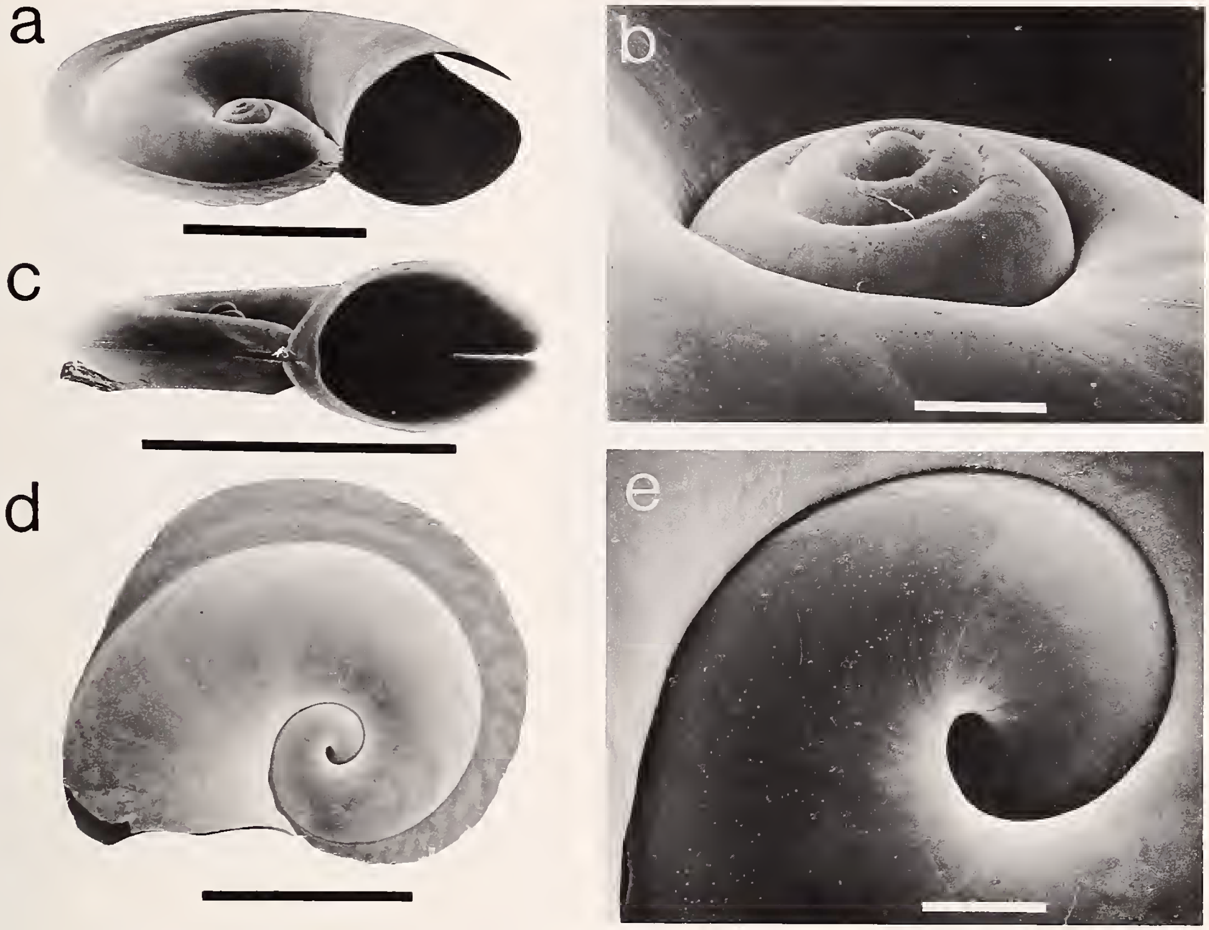


Figure 2

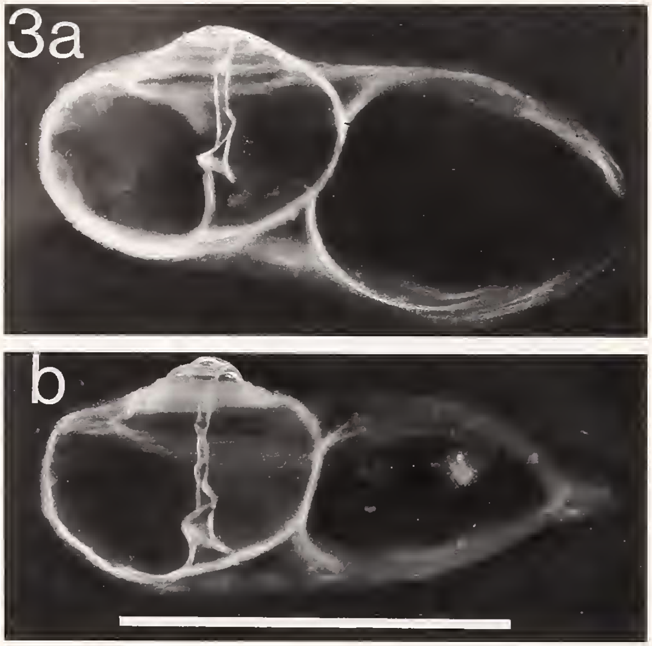
Atlanta ***californiensis*** sp. nov. a, b. Shell of holotype tilted at 50° angle. c. Apertural view of shell (1.6 mm male). d, e. Shell of paratype viewed from left side (2.1 mm male; SBMNH 140127). SEM photographs. Scale bars = a, c, d: 1.0 mm; b, e: 0.1 mm.

Description: *Shell* (Figures 1–3)—Shell moderately small; maximal diameter 3.5 mm, with 4⅔ whorls. Keel penetrates between last and penultimate whorls in shells with diameter greater than about 2.0 mm (Figure 1). Keel base color orange-brown to red-brown. Spire low conical to globular in profile, lacking surface sculpture (Figure 2a–c). Spire coloration variable; either (a) clear to uniform light yellow, brown, or violet, or (b) light to dark mottled pattern of yellow-brown to brown. Spire suture coloration variable, ranging from clear to light violet to purple. Umbilicus wide, but narrows rapidly with penultimate whorls (Figure 2d, e). Inner walls of spire decalcified, whorls divided internally by thin, flexible chitinous membrane (Figure 3a). Larval metamorphosis occurs at shell diameter of 0.5–0.6 mm.

Operculum (Figure 4)—Operculum type "c" (after RICHTER, 1974); thin, transparent, oval in shape, with monogyre nucleus. Spiral portion of operculum lacks spines.

Eyes (Figure 5a)—Eyes type "a" (after RICHTER, 1974); relatively small; clear, spherical lens; black pigmented base interrupted dorsally by triangular-shaped, unpigmented window. Distal portion of pigmented base lacking clear, transverse slit seen in type "b" eyes (Figure 5b).

Radula (Figures 6–8)—Radula large (relative to size of the animal), elongate and narrowly triangular; distinct sexual dimorphism. In males with shell diameter of 1.7–1.8 mm, length of radula about 700 μm, maximal width about 220 μm, with 75–80 rows of teeth and growth angle about 20–22°. In largest male examined (shell partially destroyed and shell diameter unknown), radula length almost 1000 μm, maximal width 260 μm, with 99 rows of teeth (Figure 6a). In male radula (Figure 7), central (rachidian) tooth with broad, low basal plate and relatively short single cusp that is always present. Lateral tooth with very broad, slightly curved basal plate, with one strong cusp at inner margin that points posteromedially. Squarish promontory of basal plate (characteristic of Atlantidae) forms a flattened hook at its posterior edge. Inner and



Explanation of Figures 3 and 4

Figure 3. Shells of a, *Atlanta* ***californiensis*** sp. nov., and b, *A. inflata* (from tropical Atlantic). Immature specimens, frontal views. Transmitted light photographs. Scale bar = 0.5 mm.

Figure 4. *Atlanta* ***californiensis*** sp. nov. "type c" operculum with monogyre nucleus (from 2.2 mm male). Transmitted light photograph. Scale bar = 0.5 mm.

outer marginal teeth approximately same length and somewhat shorter than corresponding lateral tooth. Marginal teeth long, slender, and gently curved toward tip, which is somewhat hooked.

In females with shell diameter of 1.7–1.8 mm, radula 700 μm in length (comparable with radulae from males of similar size), but maximal width (160–170 μm) about 55 μm less, growth angle (17–18°) about 4° less, and number of tooth rows (60–62) about 17 fewer. The major difference between radulae from mature males and females (Figure 8a, b) is width. Some differences in tooth morphology also exist; in females, basal plates of central and lateral teeth narrower, but distinctly higher, and marginal and lateral teeth shorter than in males.

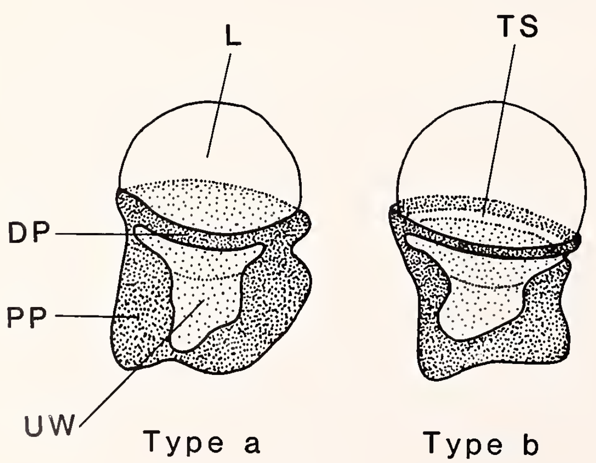


Figure 5

The two major eye types ("a" and "b") in atlantids (after Seapy, 1990a:fig. 2 and Richter, 1974:fig. 3). Key: L, lens; DP, distal pigment; PP, proximal pigment, UW, unpigmented window; TS, transverse slit.

Type material: Holotype: Shell of adult female, diameter 2.48 mm, mounted on SEM stub (Figures 1a, b, 2a, b), SBMNH 140126. **Paratypes:** Shell of adult male, diameter 1.60 mm, mounted on SEM stub (Figure 2d, e), SBMNH 140127. Preserved and dry specimens were deposited with the following museums: SBMNH 140128, 140129; CASIZ 088117, 088118; USNM 806324; and, SMF 309929, 309930.

Type locality: California, Santa Catalina Basin, 33°03.4′N, 118°24.7′W, 0–150 m.

Etymology: The specific epithet is based on the geographical distribution of the species, which is largely restricted to the California Current (see distribution below).

Remarks: *Atlanta* ***californiensis*** appears to be most closely related to *A. inflata,* a very common circumtropical species. Like *A. inflata, A.* ***californiensis*** shows partial decalcification of the inner walls of the shell spire, type "a" eye

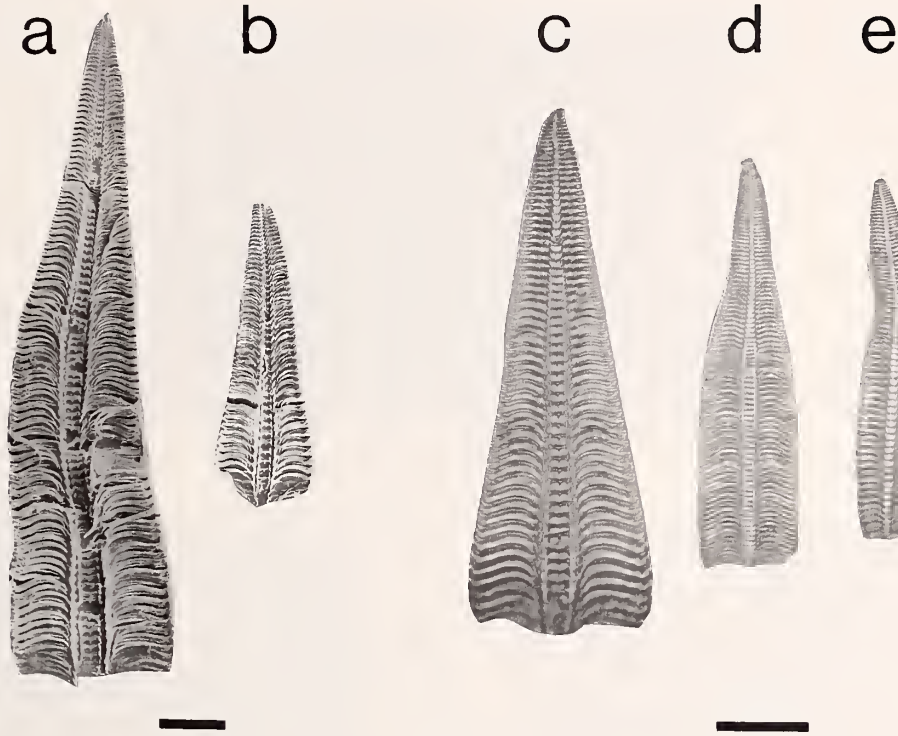


Figure 6

Complete radulae from *Atlanta* ***californiensis*** sp. nov. and *A. inflata* (from tropical Atlantic). SEM. a–c: *Atlanta* ***californiensis.*** a. Male with 99 tooth rows. b. Immature female with 56 tooth rows. c. Male with 68 tooth rows. d, e: *A. inflata*. d. Male with 98 tooth rows. e. Female with 80 tooth rows. a, b: SEM; c–e: transmitted light. Scale bars = a, b: 0.1 mm; c–e: 0.1 mm.

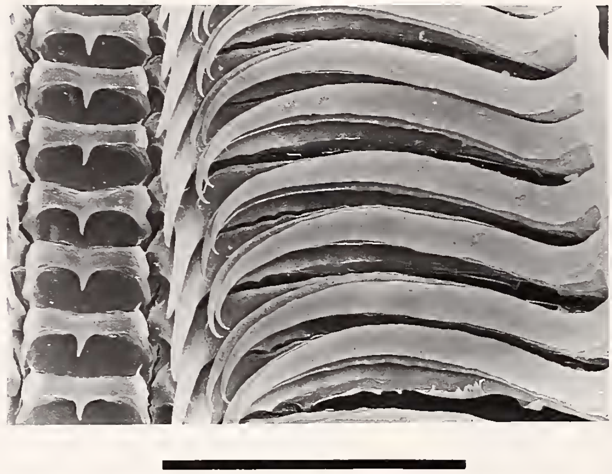
morphology, type "c" opercular morphology, sexual dimorphism of the radula, and similarities in the shape of the radular teeth and radular morphogenesis. The radulae of the two species differ, however, in that the radulae from both male and female *A.* ***californiensis*** (Figure 6a–c) are distinctly broader and consist of fewer tooth rows than the radulae of *A. inflata* (Figure 6d, e). The largest *A.* ***californiensis*** radula examined (Figure 6a) was from a large adult male and measured 1000 μm in length, with 99 rows of teeth. In contrast, the radula of the largest adult *A. inflata* examined by RICHTER (1987) was 590 μm in length, with 113 tooth rows. Although the radulae of both species are sexually dimorphic, the intersexual differences are greater in *A.* ***californiensis.***

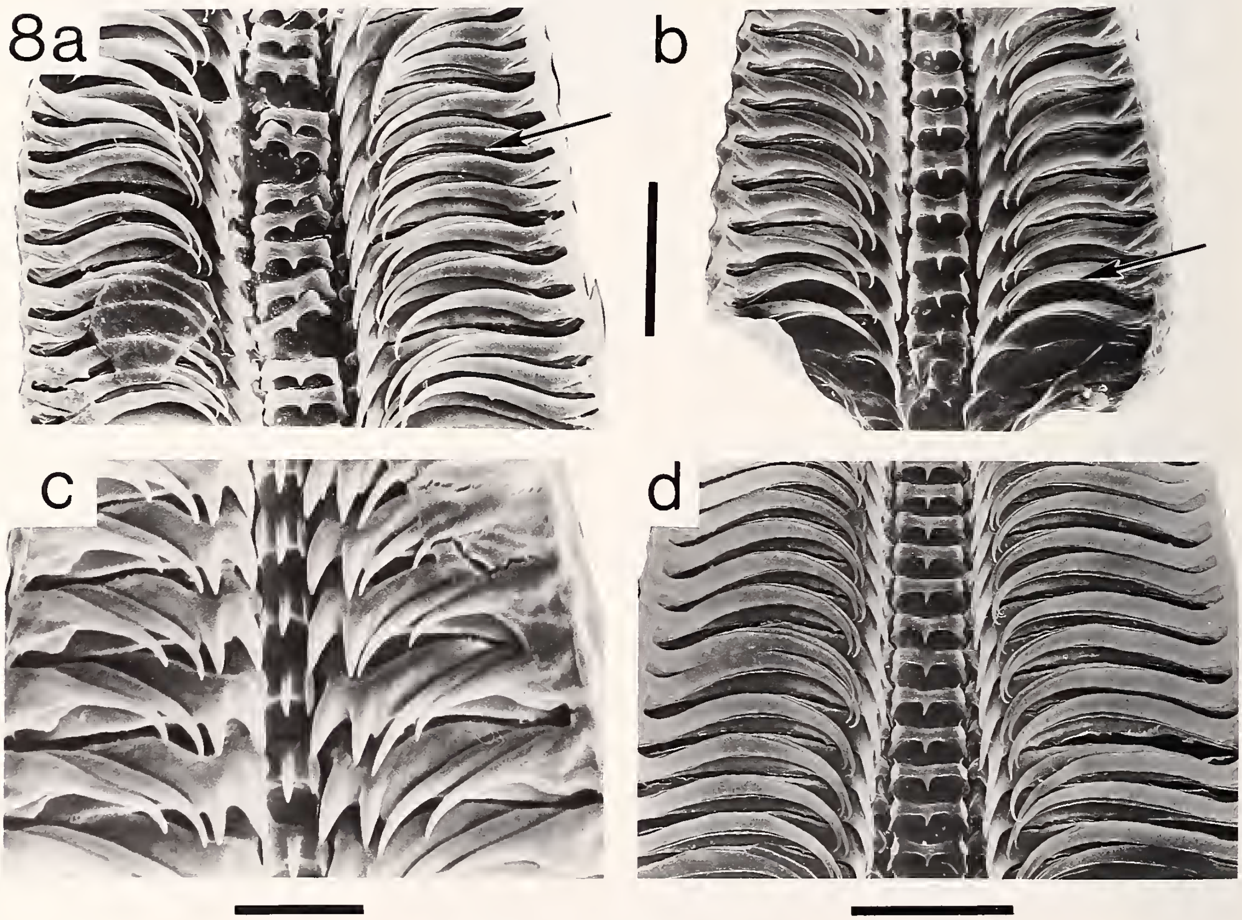
While the body and internal shell morphology of *Atlanta* ***californiensis*** are most similar to those of *A. inflata,* the external shell morphologies of the two species are quite different. The shell spire consists of about 3¼ whorls in *A.* ***californiensis*** and about 4½ whorls in *A. inflata* (Figure 9a, b). The result of this difference is that the shell diameter of a specimen of *A.* ***californiensis*** at four whorls would be more than twice that of *A. inflata* at four whorls (Figure 10). The whorls of *A.* ***californiensis*** are more inflated and grow faster than those of *A. inflata*. These differences are seen clearly by viewing the shells along the shell axis using transmitted light (Figure 3). The lack of sculpture on the spire whorls of *A.* ***californiensis*** contrasts with the raised spiral ridges on the spire of most *A. inflata* (Figure 10). This is a variable feature in *A. inflata,* however, since these ridges can be weakly expressed or even lacking (TESCH, 1909; RICHTER, 1987). Lastly, the umbilicus is wide in *A.* ***californiensis*** (Figure 2d, e) and narrow in *A. inflata* (RICHTER, 1987:figs. 9–12).

The external shell morphology of *Atlanta* ***californiensis*** is most similar to those of *A. gaudichaudi* and *A. peroni.* The three species have several features in common: (1) the shells have low spires that consist (Figure 9) of about 3¼ to 3½ whorls, (2) the shell surfaces are smooth and lack surface sculpture, and (3) the sutures between the first and second whorls are shallow, while those between subsequent whorls are deeply incised (for *A.* ***californiensis*** see Figure 1b; for *A. peroni* see SEAPY, 1990a:fig. 4g, h; for *A. gaudichaudi* see NEWMAN, 1990:fig. 2b, c). Suture pigmentation in *A.* ***californiensis*** ranges from clear (similar to *A. peroni*) to light violet to purple (similar to *A. gaudichaudi*).

Distribution: Members of the family Atlantidae (Prosobranchia: Gastropoda) are predominantly tropical to sub-

7





Explanation of Figures 7 and 8

Figure 7. *Atlanta* ***californiensis*** sp. nov. Portion of radula from mature male, including (from left to right) central (rachidian), lateral, and marginal teeth. SEM. Scale bar = 50 μm.

Figure 8. *Atlanta* ***californiensis*** sp. nov. a, b. Portions of radulae from mature male and female specimens, respectively. Arrows indicate row 60 on each radula. c, d. Morphogenesis of male radula at cross-rows 10–14 and 69–80, respectively. Photographs from different radulae. SEM. Scale bars = a, b, d: 50 μm; c: 10 μm.

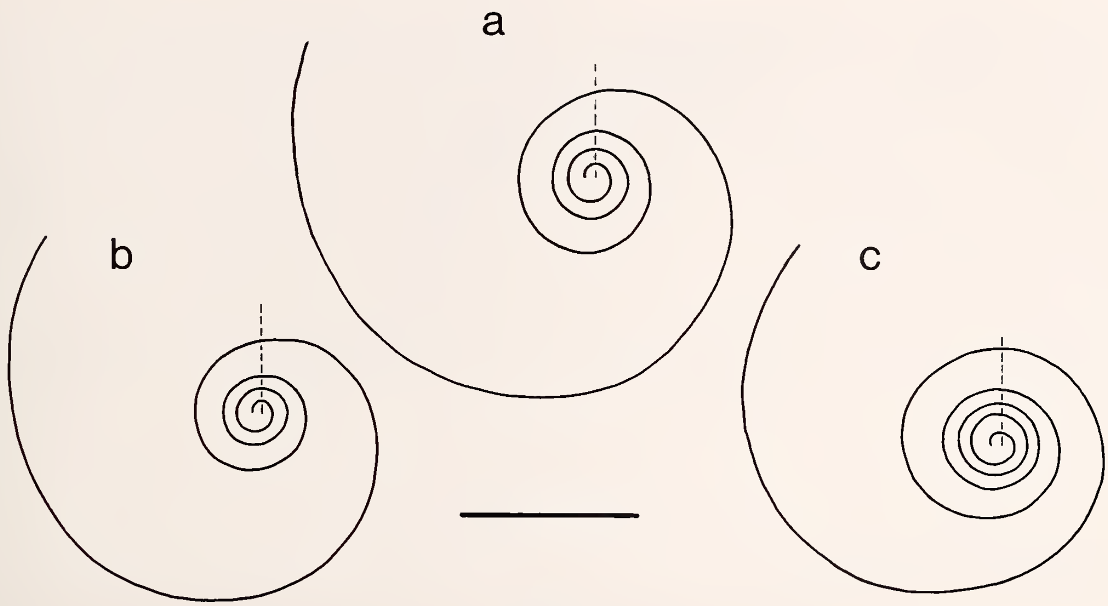


Figure 9

Sketches of shell spires from three species of *Atlanta* viewed from right side of shell. a. *A.* ***californiensis*** sp. nov. b. *A. inflata*. c. *A. gaudichaudi*. Sketches b and c after SEAPY (1990a:fig. 6). Scale bar = 0.5 mm.

tropical in distribution (THIRIOT-QUIÉVREUX, 1973). Most of the specimens of *Atlanta* ***californiensis*** collected to date, however, have come from temperate waters of the California Current off the coast of southern California. The California Current is a broad, sluggish and cold current that warms gradually as it flows southward off the Pacific coast of North America. Tropical to subtropical species of atlantids are encountered commonly only in the southern portion of the California Current, south of about 34°N (McGOWAN, 1967).

Biogeographically, the California Current comprises the southeastern portion of the Transition Zone faunal province (Figure 11). This faunal province corresponds to the Transitional Domain of DODIMEAD *et al.* (1963), and extends southeastward in the California Current, northeastward in the Alaskan Current (to about 50°N) and westward across the North Pacific Ocean to Asia in a narrow (1–2° latitude) band located to the north of the Subarctic Boundary at about 40–41°N. The Transition Zone faunal province is bounded (Figure 11) by the Subarctic Pacific faunal province to the north, the Central North Pacific faunal province to the south, and the North American Continent to the east (FAGER & McGOWAN, 1963; McGOWAN, 1986).

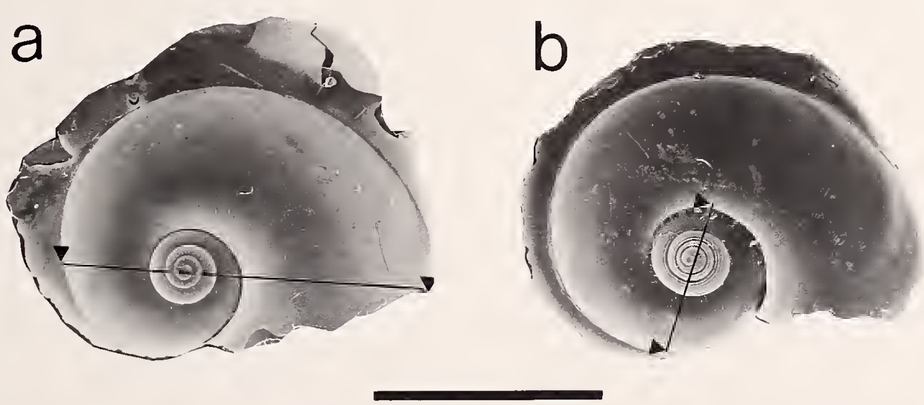


Figure 10

Shells of a, *Atlanta* ***californiensis*** sp. nov., and b, *A. inflata* (from tropical Atlantic). Lines between triangular marks indicate shell diameter at four whorls. SEM. Scale bar = 1.0 mm.

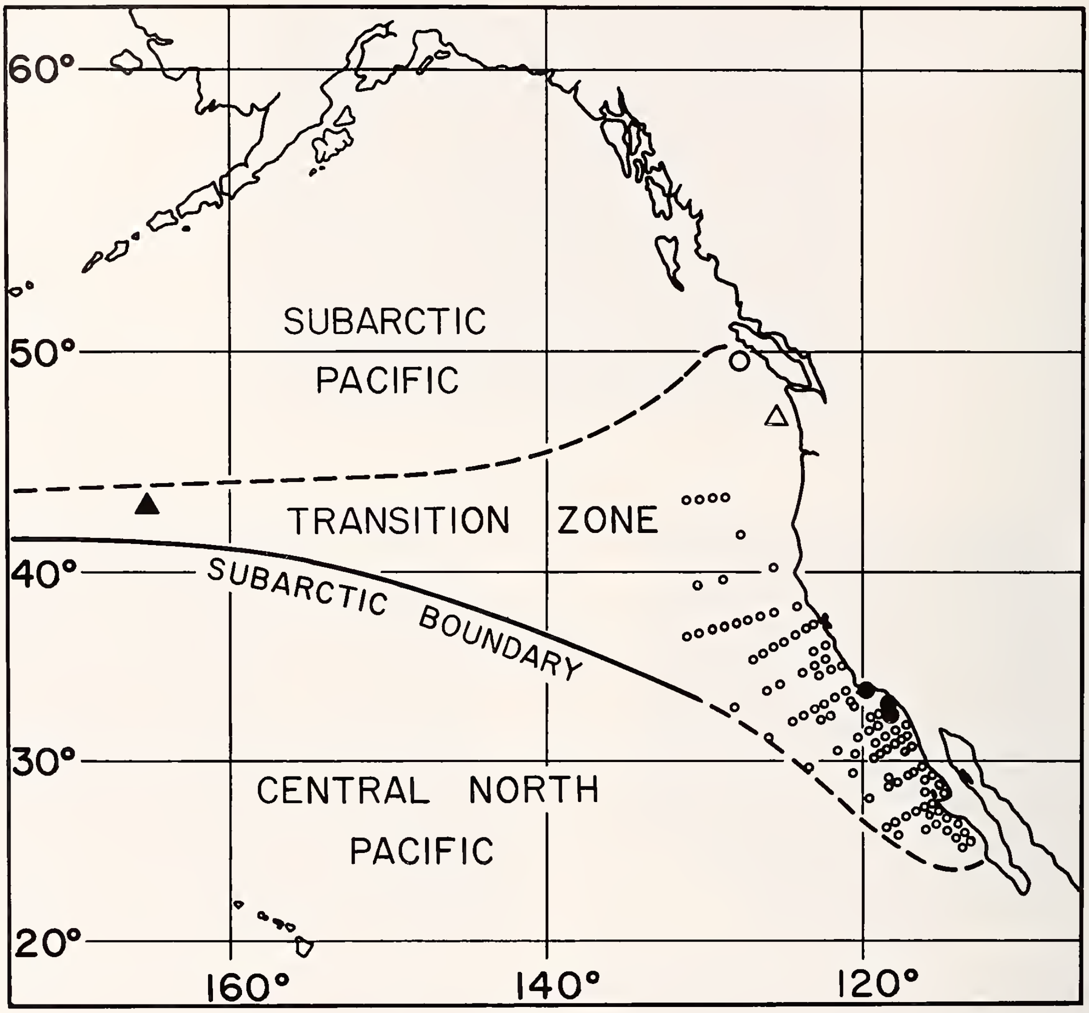


Figure 11

Biogeographical faunal provinces (Subarctic Pacific, Transition Zone and Central North Pacific) in the eastern North Pacific Ocean. Solid line denotes the Subarctic Boundary (after DODIMEAD *et al.*, 1963). Northern limits of Transition Zone indicated by dashed line (based on DODIMEAD *et al.* (1963:fig. 216). Southern limits of the Transition Zone defined by Subarctic Boundary and its southeasterly extension to Baja California (shown by dashed line; based on euphausid distribution patterns in BRINTON, 1962). Collection records for *Atlanta* ***californiensis*** sp. nov.: large solid circles = southern California (San Pedro, Santa Catalina, and Santa Barbara basins); large open circle = oceanic waters off British Columbia; solid triangle = oceanic waters north of Subarctic Boundary. Open triangle = report of KOZLOFF (1987) for "*A. gaudichaudi*" from oceanic waters off Washington. Small open circles = records of McGOWAN (1967) for *Atlanta* sp. from the California Current region off Pacific coast of North America.

Specimens of *Atlanta* ***californiensis*** have been identified by RRS from Transition Zone waters to the north of the Subarctic Boundary, oceanic waters off British Columbia, and three areas off southern California—San Pedro Basin, Santa Catalina Basin and Santa Barbara Basin (Figure 11). KOZLOFF (1987:208) reported that *A. gaudichaudi* "may be expected in oceanic plankton" off Washington. However, he qualified the identification by stating that it was "perhaps a form of *A. peroni*," although this remark could be based on a similar statement about *A. gaudichaudi* made by TESCH (1949:17). Because *A. gaudichaudi* was not recorded by McGOWAN (1967) from California Current waters north of about 33°N and the shell of *A.* ***californiensis*** is most similar to this species (see above), we are reasonably certain that the species identified by KOZLOFF (1987) as *A. gaudichaudi* is actually *A.* ***californiensis.***

The records of McGOWAN (1967) for *Atlanta* sp. are included in Figure 11 because we consider that a large proportion of the specimens (certainly those collected north of about 34°N) that were relegated by McGowan to *Atlanta* sp. were *A.* ***californiensis.*** Our reasoning for this conclusion follows. Among the atlantids reported by McGOWAN (1967) from the California Current, the only species that ranged to the north of 34°N were *Atlanta* sp. and *A. peroni.*

It is conceivable that McGowan misidentified *A. **californiensis*** as *A. peroni* under certain conditions (shells clear, spire and suture pigmentation absent), since the general shell morphologies of the two species are similar in that the spires consist of about 3¼ whorls and lack sculpture (discussed above). It is probable, however, that McGowan identified most *A. **californiensis*** as *Atlanta* sp., since most *A. **californiensis*** can be distinguished from *A. peroni* on the basis of spire coloration (normally clear, but occasionally light pink in *A. peroni* [Seapy, 1990a]; yellow, brown, or violet, often with a mottled pattern in *A. **californiensis***) and keel base coloration (clear, becoming golden-brown in *A. peroni* [Seapy, 1990a]; orange-brown to red-brown in *A. **californiensis***).

Based on the collection records in Figure 11, *Atlanta **californiensis*** is clearly a Transition Zone species. We are not aware of any records for *A. **californiensis*** from Subarctic Pacific or Central North Pacific waters. No collection records for any species of atlantids exist to our knowledge from Subarctic Pacific waters, and extensive collections of atlantids from Hawaiian waters (Seapy, 1990a) have never recorded *A. **californiensis***. A Transition Zone distribution has been characterized previously for only one other species of heteropod, *Carinaria japonica* (Seapy, 1974).

The vertical distribution of *Atlanta **californiensis*** has not been resolved in detail. However, based on samples collected with opening-closing BONGO nets in San Pedro Basin (Seapy, unpublished data), the daytime vertical range appears to be largely limited to the epipelagic zone (surface to about 150 m off southern California). Opening-closing net samples have not been collected at night, and the question of whether or not nocturnal vertical migration takes place in this species remains to be determined. However, we suspect that upward nocturnal migration does occur since vertical migration was reported (Seapy, 1990b) for other species of atlantids whose ranges also extended into the lower portion of the epipelagic zone off Hawaii.

An interesting aspect of the vertical distribution of *Atlanta **californiensis*** is that large numbers of individuals have been collected in surface samples taken with neuston nets on a number of occasions in San Pedro Basin (Seapy, unpublished data). The animals in these samples were exclusively males. Similar observations of high densities of male heteropods in the neuston were made by Richter (unpublished data) for three species—*Protatlanta souleyeti* (Smith, 1888), *A. oligogyra* Tesch, 1908, and *Firoloida desmaresti* Lesueur, 1817—during Cruise 51 of the R/V *Meteor* in the central, tropical Atlantic Ocean during 1979. Heteropods are relatively uncommon in the neuston, but we have found that when they occur in high abundances most (if not all) of the individuals are mature males. These males do not appear to assemble in the uppermost water layer for feeding purposes, since their guts are usually empty (Richter, unpublished data). Perhaps this behavior is similar to that seen in mosquitoes, black flies, and other dipterans that exhibit aerial mating (reviewed by Downes, 1969). Males assemble in large swarms and individual females enter the swarm briefly to be captured by a male, drop out of the swarm, and mate. This behavior functions to bring the sexes together from dispersed populations.

Discussion: *The radula as a taxonomic character*—The utility of the radula as a taxonomic character in the Atlantidae has been questioned and rejected by a number of workers (see below). We suggest that this rejection has resulted from a lack of understanding of radular ontogenesis. Since the teeth that are produced first are not cast off from the anterior end of the radula as they outwear their use, all growth stages of the radula are present in mature animals. As a consequence, the number of tooth rows increases continuously as the animal grows.

Because the shapes of the radular teeth change dramatically during ontogenesis, the radular characterizations given above apply exclusively to the mature portions of adult radulae. In most gastropods, morphogenesis of the radular teeth during ontogeny is restricted to the first few rows of teeth in the larval and post-larval animals (Sterki, 1893). In the Atlantidae, however, the transformation of tooth shapes continues for the greater part of radular growth (Richter, 1961, 1963).

The following characterization of morphogenetic changes in the radular teeth of *Atlanta **californiensis*** are applicable in principal to other atlantids. The teeth that are initially produced in the larva include a central rachidian tooth with a more-or-less square basal plate and a long, strong cusp. The corresponding lateral teeth are short and bi-, tri-, or even polycuspid. There is only one short marginal tooth on either side of the lateral teeth. In about rows 7 to 10 the second (outer) marginal teeth appear and the radula by now shows the regular taenioglossate tooth formula of $M_2M_1LRLM_1M_2$ (Figure 8c). At this stage of radular growth, there are no differences between males and females. The lateral teeth are strongly bicuspid and a rudimentary third cusp is present, but the third cusp disappears completely in the next few rows. The second (outer) cusp of the lateral teeth gradually decreases in size to an accessory denticle and then disappears altogether by about rows 50 to 60, generally later in females than in males. However, in males the teeth continue to change and attain their final shape after an additional 10 to 20 rows (Figure 8d).

From the above description of radular morphogenesis, it is clear that only the adult portion of the radula should be used as a taxonomic tool and that radular morphology is nearly useless when applied to juvenile specimens. Earlier workers presumably did not appreciate the complexities of radular morphogenesis, which would explain why a number of them (*e.g.*, Buchmann, 1924; Tesch, 1949; van der Spoel, 1976) concluded that the radula is of no taxonomic importance in the Atlantidae.

ACKNOWLEDGMENTS

The specimens used in this study were largely collected from southern California waters by plankton and neuston nets deployed from the R/V *Yellowfin* of the Ocean Studies Institute, California State University. We are grateful to

Captain J. Cvitanovich and the crew of the *Yellowfin* for their help. A. L. Alldredge, University of California, Santa Barbara, provided a series of plankton samples from the 1990 "Spirit" cruise in Santa Barbara Basin. D. L. Mackas, Institute of Ocean Sciences, British Columbia, forwarded a series of plankton samples from the Institute's zooplankton archives. K. Bigelow, National Marine Fisheries Service, Honolulu, Hawaii Laboratory, observed atlantids in a plankton sample collected from Subarctic Boundary waters and forwarded the specimens to RRS. The manuscript has been greatly improved by the reviews of several early drafts by F. G. Hochberg, Jr., Santa Barbara Museum of Natural History, Santa Barbara, California. We thank S. Karl for SEM operation, photography, and printing of Figures 1 and 2.

LITERATURE CITED

BRINTON, E. 1962. The distribution of Pacific euphausiids. Bulletin of the Scripps Institution of Oceanography 8:51–270.

BUCHMANN, W. 1924. Über den Pharynx der Heteropoden. Zeitschrift für Anatomie und Entwicklungsgeschichte 73: 501–540.

DODIMEAD, A. J., F. FAVORITE & T. HIRANO. 1963. Salmon of the North Pacific Ocean. Part II. Review of Oceanography of the Subarctic Pacific Region. International North Pacific Fisheries Commission, Bulletin 13. 195 pp.

DOWNES, J. A. 1969. The swarming and mating flight of Diptera. Annual Review of Entomology 14:271–298.

FAGER, E. W. & J. A. MCGOWAN. 1963. Zooplankton species groups in the North Pacific. Science 140:453–460.

KOZLOFF, E. N. 1987. Marine invertebrates of the Pacific Northwest. Seattle: University of Washington Press. 511 pp.

MCGOWAN, J. A. 1967. Distributional atlas of pelagic molluscs in the California Current region. California Cooperative Fisheries Investigations, Atlas 6. 218 pp.

MCGOWAN, J. A. 1986. The biogeography of pelagic ecosystems. Pp. 191–200. *In* A. C. Pierrot-Bults, S. van der Spoel, B. J. Zahuranec & R. K. Johnson (eds.), Pelagic Biogeography. Proceedings of an International Conference. The Netherlands 29 May–5 June 1985. UNESCO Technical Papers in Marine Science, Number 49.

NEWMAN, L. J. 1990. The taxonomy, distribution and biology of *Atlanta gaudichaudi* Souleyet, 1852 (Gastropoda, Heteropoda) from the Great Barrier Reef, Australia. American Malacological Bulletin 8:85–94.

RICHTER, G. 1961. Die Radula der Atlantiden (Heteropoda, Prosobranchia) und ihre Bedeutung für die Systematik und Evolution der Familie. Zeitschrift für Morphologie und Ökologie der Tiere 50:163–238.

RICHTER, G. 1963. Untersuchungen zur Morphogenese der Gastropodenradula. Pp. 142–152. *In:* F. Leuwer (Kommissionsverlag), Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven. Drittes meeresbiologisches Symposion.

RICHTER, G. 1974. Die Heteropoden der "Meteor"-Expedition in den Indischen Ozean 1964/65. "Meteor" Forschung-Ergebnisse, (D)17:55–78.

RICHTER, G. 1987. Zur Kenntnis der Gattung *Atlanta* (III). *Atlanta inflata, A. helicinoides, A. echinogyra* und *A. plana* (Prosobranchia: Heteropoda). Archiv für Molluskenkunde 117:177–201.

SEAPY, R. R. 1974. Distribution and abundance of the epipelagic mollusk *Carinaria japonica* in waters off Southern California. Marine Biology 24:243–250.

SEAPY, R. R. 1990a. The pelagic Family Atlantidae (Gastropoda: Heteropoda) from Hawaiian waters: a faunistic survey. Malacologia 32:107–130.

SEAPY, R. R. 1990b. Patterns of vertical distribution in epipelagic heteropod molluscs off Hawaii. Marine Ecology Progress Series 60:235–246.

SPOEL, S. VAN DER. 1976. Pseudothecosomata, Gymnosomata and Heteropoda. Utrecht (Bohn, Scheltema and Holkema). 484 pp.

STERKI, V. 1893. Growth changes in the radula in land molluscs. Proceedings of the Academy of Natural Sciences of Philadelphia 1893:388–400.

TESCH, J. J. 1909. Systematic monograph of the Atlantidae with enumeration of the Leyden Museum. Notes of the Leyden Museum 30:1–30.

TESCH, J. J. 1949. Heteropoda. Dana Report 34. 53 pp.

THIRIOT-QUIÉVREUX, C. 1973. Heteropoda. Oceanography and Marine Biology Annual Review 11:237–261.